



## Invited Commentary

### Many avenues for spatial personality research: a response to comments on Stuber et al. (2022)

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We are grateful for the thought-provoking and forward-looking commentaries (Dingemans et al. 2022; Mabry 2022; Spiegel and Pinter-Wollman 2022; Vander Wal et al. 2022) in response to our meta-analysis of evidence for consistent among-individual differences in animals' spatial behaviors (Stuber et al. 2022). A clear consensus is that our demonstration of the prevalence of repeatability across spatial behaviors, and taxa, is only the first step towards identifying the mechanisms and consequences of variation in spatial behavior. Here, we take the opportunity to emphasize key future directions pertaining to uncovering mechanisms, disentangling apparent personality from spatial constraints, and examining additional metrics of variation.

### TOWARD A MECHANISTIC UNDERSTANDING OF INHERENT SPATIAL PERSONALITY

All commenters highlight potential avenues to understand the genetic, physiological, behavioral, and ecological factors underlying repeatable differences in spatial behavior. For example, Spiegel and Pinter-Wollman (2022) highlight that quantifying variation in movement while accounting for local environmental conditions and individuals' prior experience, physiology, or morphology will illuminate potential pathways for apparent or actual movement personality to arise. Vander Wal et al. (2022) suggest quantifying behavioral reaction norms as an approach to determine spatial behaviors' place within an adaptive evolutionary framework. Quantifying behavioral reaction norms will help isolate the impacts of environmental constraints, link consistent differences in behavior to variation in fitness, and advance our understanding of adaptive capacity and evolution of spatial behavior. Finally, both Dingemans et al. (2022)

and Mabry (2022) highlight the importance of measuring individuals' behavior over time as a way to separate the effects of parents' spatial decisions from their offspring's. Longitudinal studies can quantify the scope for reversible plasticity, which enables populations to respond to environmental change over relatively short timespans. We agree that these pathways and others successfully used to investigate "traditional" personality traits can be productively applied to the study of spatial personality.

### ENVIRONMENTAL CONTEXT AS TRAIT OR CONSTRAINT?

We noted that our meta-analytic approach precludes the separation of consistent differences in environmental preference from differences in constraints on the availability of environmental gradients. When given access to a full landcover mosaic, for example, individuals may prefer to spend time in particular landcover types for various reasons, leading to apparent differences in other behaviors, such as mean step length and travel speed (e.g., if different environments are more easily traversed than others). Inversely, individuals may consistently differ in behaviors due to stable differences in morphology, leading to apparent differences in environmental preferences (e.g., if different movement behaviors are more efficient in certain environments). Mabry (2022), Spiegel and Pinter-Wollman (2022), and Vander Wal et al. (2022) all suggest that the environmental context experienced by individuals can constrain spatial behavior and suggest future studies account for local environment when investigating spatial personality. We agree that this is an important step; however, we emphasize that environmental preferences may themselves be a type of personality and represent an equally viable alternative hypothesis that should be tested. We agree with Vander Wal et al.'s (2022) sentiment that identifying which traits are independent, and which traits form behavioral syndromes is an important early step that will in turn inform whether traits are correlated because one is a consequence of the other or because they arise from similar underlying mechanisms. As Spiegel and Pinter-Wollman (2022) suggest, disentangling these alternatives will be challenging, but nevertheless important.

### VARIATION AS A MULTIDIMENSIONAL CONCEPT

Dingemans et al. (2022) and Vander Wal et al. (2022) rightly note that repeatability is only a starting point for understanding variation in individual behavior. Repeatability itself is an aggregate metric combining among- and within-individual variance, which includes measurement error. Dingemans et al. (2022) caution that meaningfully comparing repeatability across datasets can be difficult. In particular, measurement error can bias repeatability estimates if

not taken into account. Trickier yet, disparate behavioral metrics may be associated with systematically different amounts of measurement error, which will at best add noise to comparative patterns in repeatability and at worst bias these patterns. Although none of the studies included in our meta-analysis formally quantified measurement error, a coarse post hoc examination of the effects of locational measurement error on repeatability revealed no significant relationship. However, we note that home range size estimates were systematically measured with the highest locational uncertainty, and movement behaviors the lowest. Nevertheless, Dingemanse et al. (2022) propose the coefficient of variation (CV) as an alternative metric for comparative studies of variation. Although CV has attractive properties, it is limited by the types of variables it can be applied to, and its validity when trait variance does not scale proportionally with the mean, when traits follow different distributions or vary in dimensionality, and its sample size dependence (e.g., Taylor 1961; Smithson 1982; Einum et al. 2012; Pélabon et al. 2020). Both repeatability and CV summarize different information on variability, and thus can be viewed as complementary where studying multiple metrics and components of variation will provide the most complete information on trait variation (Dingemanse et al. 2022).

## CONCLUSION

Taken together, our meta-analysis and its commentaries highlight the need for research that investigates both among- and within-individual variation to uncover induced versus inherent drivers shaping variation in spatial behaviors (Spiegel and Pinter-Wollman 2022). Understanding links among variation in spatial behavior, fitness, and heritability will identify likely paths for phenotypic evolution (Vander Wal et al. 2022). Quantifying behavioral variation will reveal traits harboring reversible plasticity (Dingemanse et al. 2022), and the extent of developmental plasticity (Mabry 2022). Both among and within species, variation is vital to maintain functional populations under environmental change; considering the magnitude of change associated with the Anthropocene, the timing is apt for behavioral variation to play a greater role in spatial and

landscape ecology as we begin to incorporate concepts of behavioral and evolutionary ecology to our understanding of species' response to changing environments.

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